

Chironomus utahensis Malloch and *Chironomus harpi* new species
and their karyosystematic relationships to other species in the
decorus-group of *Chironomus*

(Chironomidae: Diptera)

By W. Wülker, J. E. Sublette and J. Martin

Wülker, W., J. E. Sublette and J. Martin (1991): *Chironomus utahensis* Malloch and *Chironomus harpi* new species and their karyosystematic relationships to other species in the *decorus*-group of *Chironomus* (Chironomidae: Diptera) – Spixiana 14/1: 71–94.

Adult, pupal and larval morphology and karyotypes of *Chironomus utahensis* Malloch and *Chironomus harpi*, spec. nov. are described.

Adults of *C. utahensis* resemble *Chironomus atrella* (Townes) and *C. anthracinus* Zetterstedt; however, the resemblance is apparently from convergence. The dark coloration, clypeus narrower than the antennal pedicel, long foretarsal beard, short, rather broad, pale anal point and the almost straight superior volsella will differentiate it from other members of the genus. Adults of *C. harpi* most closely resemble *C. decorus* Johannsen and *C. maturus* Johannsen but the male genitalia are distinctive in having an almost straight superior volsella which is blunt tipped and a narrower anal point with a weakly delimited tongue-like apical lobe.

While the larvae and pupae of the Nearctic *Chironomus* are still inadequately known, the dark antennal pedicel of the larval *C. utahensis* appears to be a distinctive feature.

Karyosystematically, *C. utahensis* and *C. harpi* are closely related. Although none of the seven chromosome arms is identical in both species, the banding patterns can be derived by only a few inversion differences. Both species belong to a karyosystematically defined, possibly monophyletic „*decorus*-group“ in which at least *C. utahensis* has a relatively basal position. Inversion polymorphism has been recorded in chromosome arms A, C, D, E, F and G of *C. utahensis* whereas in *C. harpi* only an inversion in arm G has been found.

Chironomus utahensis lives in ponds and lakes in western North America. *C. harpi*, known from Arkansas, Missouri, Illinois, and New York in USA, and New Brunswick in Canada, inhabits saline or acid lentic biotopes.

Prof. Dr. Wolfgang Wülker, Institut für Biologie I (Zoologie) der Universität, Albertstraße 21 a, D-7800 Freiburg, F.R.G.

Prof. Dr. James E. Sublette, Department of Life Sciences, University of Southern Colorado, 2200 Bonforte, Pueblo, CO 81001, U.S.A.

Dr. Jon Martin, Department of Genetics, University of Melbourne, Parkville, Victoria, 3052, Australia.

Introduction

Chironomus utahensis was described by Malloch in 1915 from Utah, USA. It is widely distributed in the western part of the United States and is also recorded from Canada. Townes (1945) reported the species from Alberta, California, Colorado, Minnesota, Nevada, Oregon, and Utah; Schaller and English (1976) found it in Arizona; Sublette and Sublette (1979) and Martin et al. (1979) added some localities in New Mexico and South Dakota. In this paper we also report the species from North Dakota, Montana, and Wisconsin.

The adult of *C. utahensis* is a more or less unspecialized, moderately large, blackish species with a long tarsal beard and a short, rather broad, amber colored anal point in the male (Townes 1945). The larva has a conspicuous dark pedicel to the antenna.

While investigating the hemoglobins in the larval hemolymph, Schaller and English (1976) published a photograph of a set of salivary gland chromosomes and were hopeful that comparisons of hemoglobins and chromosome banding patterns with those of other chironomid species would help to clarify their taxonomic and evolutionary relationships. Martin et al. (1979) made an initial attempt to analyze the banding patterns of the seven chromosome arms but left a complete analysis "until the near relatives can be studied." Nevertheless, they saw the typical inversion 9-2 in arm F and stated this to be similar to *C. obtusidens* Goetghebuer and *C. decorus* Johannsen. In another paper, Martin (1979) tentatively placed *C. utahensis* in close relationship to the *decorus*-group species studied (as *C. tentans*, misdet.) by Blaylock (1963, 1965).

In this present paper, we give a detailed morphological and karyosystematic description of *C. utahensis* which consolidates it as belonging to a karyosystematically defined "*decorus*-group," i. e. a group of species related by chromosome sequences rather than by adult morphology, as in the various species that are *decorus*-like as adults. The *decorus*-group is also dissimilar to the previously defined cytological groups of Keyl (1962), Martin et al. (1974), and others, in that it does not represent a group of species with a unique combination of chromosome arms. Rather, all members of this group belong to the *thummi*-complex (i. e. arm combination AB, CD, EF, G) with respect to the arm combination. Furthermore, *C. utahensis* appears to be closely related to a new species, *C. harpi*, described herein, which has been found in Arkansas, Missouri, Illinois, New York, and New Brunswick, and is apparently a specialized inhabitant of acid or saline waters (Bates and Stahl 1985).

Material and Methods

Material examined: Unless indicated otherwise, the material reported upon in this study are in the second authors collections. Specimens from the following museums were examined (abbreviations in parenthesis):

- CIS - California Insect Survey
- USNM - U. S. National Museum of Natural History, Washington, D. C.
- UCR - University of California, Riverside
- CAS - California Academy of Sciences, San Francisco
- KU - Kansas University, Lawrence
- UMo - University of Missouri, Columbia
- FWI - Freshwater Institute, Winnipeg
- INHS - Illinois Natural History Survey, Urbana

a) *Chironomus utahensis*

CALIFORNIA

Contra Costa Co., Antioch, 6-IV-1956, W. Wasbauer - 4 males (CIS); West Pittsburg, 11-II-60, J. Powell - 9 males (CIS).

Inyo Co., L. Crowley Bishop, 11-VI-49, P. R. Needham – 6 males (USNM); 6-IV-49, R. Niedman – 7 males (USNM).

Lassen Co., 1.3 mi. W Litchfield, 25-XII-67, J. Martin, UC. 10.2 – 2 males, 1 female; Westwood, 16-V-48, W. W. Wirth – 1 male (USNM).

Los Angeles Co., Lancaster, 17-V-62, L. D. Anderson – 37 males (UCR); 3-VII-62, J. Sugarman – 4 males (UCR).

Modoc Co., Stranghold, 17-VII-48, W. W. Wirth – 1 male (USNM); 2 mi. E. Canby, 12-VII-47, Usinger – 2 males (CAS).

Mono Co., Convict Creek, 17-VII-63, H. D. Kennedy. – 1 male, 1 larval exuvia (USNM); 1.7 miles E., Benton Hot Springs, 21-VIII-67, J. Martin, U. C. 1.1., 1 male, 1 pupa, 2 pupal exuviae, 14 chromosome squashes (USNM); Topaz, 7-X-17 – 1 male (USNM).

Plumas Co., Lake Davis, 1-V-68, G. Grodhaus, lot D – 6 males, 1 female; 3.5 miles SW Storrie, 1-V-68, Te68-63, G. Grodhaus -progeny of female: 1 male, 1 pupa, 1 pupal exuvia, 1 larva, 2 squashes.

San Bernardino Co., Spring Valley Lake, 11-VII-1973, M. Mulla – 1 male; Spring Valley Lake near Hesperia, Apple Valley, 23-V-71, E. C. Bay – 1 male (UCR); Fish hatchery nr Spring Valley Lake, Apple Valley, IX-76, S. Frommer & W. Wülker, 10 squashes; Silver Lake, S. Frommer, 10 squashes.

Siskiyou Co., Sheepy Cr., 27-VI-64 – 6 males (USNM); Tule Lake, 25-V-58, A. M. Barnes – 9 males.

MONTANA

Lake Co., Ronan, 2 mi. S, 9-VIII-68, alkaline pond, J. E. Sublette – 8 pupae, 8 larval exuviae, 47 squashes; 21-VIII-68 J. E. Sublette – 4 larvae, 4 pupal exuviae, 8 pupae.

NEW MEXICO

Colfax Co., Drainage ditch, 3 mi. N. Charette Mesa, 12-VIII-65, D. Ikenberry – 18 males; Eagle Nest Lake, 10-X-70, Jon Martin, M. Beard – 5 males, 2 females, 1 pupa, 1 larva, 41 squashes; 12-XI-70, J. Martin, M. Beard – 4 males, 1 pupae, 2 pupal exuviae; 20-XI-70, J. Martin, M. Beard – 28 males, 1 female, 1 pupa, 5 pupal exuviae; XII-70, egg mass # 1, J. Martin, M. Beard – 2 male, 1 pupa, 1 pupal exuvia, 1 larval exuvia; no date, egg mass # 2 – 1 pupa, 1 larva, 1 squash; 8 mi. W. Maxwell, Stubblefield Lake, 11-VIII-65, D. Ikenberry – 12 males; Miami Lake, 10-VIII-65, at light, D. Ikenberry – 16 males, 2 females, 1-IX-65, reared – 2 males, 2 pupal exuviae, 2 larval exuviae, 12 squashes; Mineral Springs at Taylor Springs, 3-XI-74, M. Beard – 77 squashes; Springer Lake, 4.2 mi. NW Springer, 9-VIII-65, D. Ikenberry – 18 males, 2 females, 5 pupal exuviae, 5 larval exuviae.

Harding Co., Upper Abbott Lake, 11-X-70, J. & H. I. Martin and M. Beard, UNM-5-4 – 84 males, 27 squashes; 16-X-70, J. & H. I. Martin and M. Beard, UNM-5-4 – 1 male; 28-XI-70, J. & H. I. Martin and M. Beard, UNM-5-5 – 3 males, 1 female, 4 pupal exuviae, 1 larval exuvia, 15 squashes.

Mora Co., Charette Lake, 12-VIII-65, D. Ikenberry – 16 males; Charette Lake, 22-VIII-67, W. R. Atchley, J. Willis – 79 males, 5 females.

Roosevelt Co., Dora, 1-IV-64, J. E. Sublette – 3 males, 2 females, 1 pupa, 5 pupal exuviae, 5 larval exuviae; 3-IV-64, J. E. Sublette – 9 pupae, 1 female, 1 pupal exuvia, 9 larval exuviae; 10 mi. E Dora, Windmill pond, 7-IV-65, J. E. Sublette – 1 male, 1 pupal exuvia.

San Miguel Co., Morphe Lake, 7-VII-70, G. Harrell, at light – 1 male; 25-VII-70, G. Harrell, at light – 1 male; Sapello River, 28-VI-70, G. Harrell, light trap – 7 males; 28-VIII-70, G. Harrell, light trap – 1 male; Storrie Lake, 2-VII-70, G. Harrell, light trap – 35 males; 22-VII-70, G. Harrell, light trap – 60 males; 9-VIII-70, G. Harrell, light trap – 71 males; no date, G. Harrell – 1 male.

San Juan Co., La Plata River, approximately 2.5 mi. S of Colorado state line on N. M. 170, 20-VIII-76, J. E. Sublette – 1 pupa, 1 larval exuvia; Morgan Lake, S of Fruitville, 1-VII-63, Larry A. McElfresh – 2 males.

NORTH DAKOTA

Kidder Co., Crystal Springs, 10-VII-52, E. B. Hayden – 12 males (KU).

OREGON

Klamath Co., Eagle Ridge Park, 2-VI-82 – 4 males, 4 females; Klamath River, Hwy 97, 24-VI-82, light trap, 8 males; Fremont Bridge, 2-VI-82, sweep net – 1 male; Upper Klamath Lake, Lake shore, 25-VII-86 – M. A. Morstad – 3 males; 1 mi. N Williamson River, 26-VIII-67, UOR. 2.2, J. Martin – 4 males, 1 female, 61 squashes. The species is so common in this locality that it is known as the “Klamath midge” (Townes 1945)

SOUTH DAKOTA

Charles Mix Co., L. Andes, 30-VI-24, 1 male (UMo).

Campbell Co., L. Campbell, 20-VI-35, D. E. Herreman – 28 males, 24 females (UMo).

Charles Mix Co., Platte, Lake Francis Case, Platte Bay, 24-IV-1-VI-67, P. L. Hudson – 1 male.

Charles Mix Co., Pickstown, St. Phillips Bay, flooded terrestrial vegetation, 22-V-69, P. L. Hudson – 1 male, 1 pupal exuvia, 1 larval exuvia (I-WI).

Charles Mix Co., Wagner, 3 mi. S, 1 mi E, X-68, P. L. Hudson – 5 males, 15 squashes.

Yankton Co., Polluted farm pond, 4 miles N. Yankton, V-68, P. Hudson, 1 squash.

UTAH

Utah Co., Goshen, 16-VIII-40, R. H. Beamer- 1 male (KU).

Utah Co., Goshen Bay, Utah Lake, V -74, P. K. Shiozawa – 2 males.

Sanpete Co., Sevier Bridge Res., 10 mi. N Gunnison, 12-VI-52, E. B. Hayden – 39 males (KU).

6 mi. W Smithfield, 15-VI-54, G. Bohart – 1 male (KU).

WISCONSIN

Marathon Co., Cold Springs Cyn. Lake, N. Stratford, 26-IV-14, Burrell – 2 males (INHS).

b) *Chironomus harpi* Paratypes

CANADA

NEW BRUNSWICK

N. Brunswick Mines, sedimentation basin, 19-IX-68 W. K. Besch – 18 males;

Heath Steel Mines, shaft II. wall pool, 29-IX-68 W. K. Besch – 10 males.

U.S.A.

ARKANSAS

Saline Co, Bauxite open-pit lakes, 40 km SW Little Rock, G. L. Harp: Lake II, SW $\frac{1}{4}$ Section 24, T2S R14W, NE $\frac{1}{4}$, 23-V-70 – 1 male, 5 females, 7 male pupal exuviae, 1 female pupal exuvia; Lake III, SW $\frac{1}{4}$ Section 11, T2S R14W, 21-III-70 – 1 male, 1 female; 23-V-70, – 4 males, 2 males; Lake IV, T2S, R14W S11SE $\frac{1}{3}$, 21-III-70, – 1 male, 4 females; Lakes II, III, IIIa, IV, 65 squashes.

ILLINOIS

Jackson Co., Bradley's Acid Pit, III-77, K. Yamamoto, – UIL.1.1. – 1 male, 9 squashes.

NEW YORK

Orleans Co., Marsh contaminated with heavy metals, 2–2.4 km E Middleport, 28-VII-81, K. W. Simpson UNY.5.1 and UNY.5.2 – 1 male, 4 squashes.

Methods

Adults, pupae, larvae, and chromosomal squashes have been slide mounted in euparal. In most instances, larval head capsules have been mounted on the associated chromosomal squash slide. Several examples of reared and associated larva, pupa, and adult have been mounted on the same slide. Material for SEM examination has been chemically dehydrated in an ethanol-toluene series, air dried or critical-point dried, and mounted on examination stubs which were sputter-coated with gold-palladium before SEM examination.

In the larvae, size has been determined by measuring the length of the venter of the head capsule from the tip of the mentum to the postoccipital margin and is reported as the ventral head length. This dimension, in contrast to

the width of the head capsule, or total head length which have been frequently reported in the literature, is least susceptible to deformation during slide mounting.

For statistical purposes, discrete variables are presented as median values followed by range and number on which the statistic is based given in parenthesis. For continuous variables, the mean has been given followed by the range and number. In some instances where only small numbers were examined, the range only and number are given. In the description of *C. harpi* new species, the holotype variable is presented first with the statistics for the paratypes given in brackets. For the most part, morphological terminology follows Saether (1980).

The method of chromosome preparation was described by Keyl and Keyl (1959) and the identification of the chromosome arms and the standardization of banding patterns follows the system established by Keyl (1962). Some larvae had been in 3 parts ethanol: 1 part glacial acetic acid fixative for 20 years; the salivary glands from these individuals were treated in 45% acetic acid for about two minutes before chromosome squashes were made in the usual manner.

Results

Chironomus utahensis Malloch

Chironomus utahensis Malloch 1915: 438, original description (adult male). Type locality, Kaysville, Utah, USA (USNM); Eggleton 1931: 255, biology; Bonnell and Mote 1941: 324, 1942: 3, biology, brief description of eggs and larva; Schaller 1972: 1, biochemistry and cytology; Sublette and Sublette 1979: 89, distribution; Martin et al. 1979: 139, karyotype.

Tendipes (Tendipes) utahensis (Malloch), Townes 1945: 127, review; Sublette 1960: 214, distribution; Nabrotzky 1968: 12, ecology; Nabrotzky and Rees 1968: 45, ecology.

Adults

Male

Coloration. Thoracic ground color yellowish-brown to dark brown; vittae, preepisternum, and postnotum blackish-brown; abdomen largely blackish-brown; terga II-VIII with a narrow apical fascia which is slightly paler brown; genitalia dark. Coxae blackish-brown; femora and tibiae yellowish brown; tarsi largely blackish with the basal one-third of Ta_1 on PII and III slightly paler.

Head. Antennal ratio, 4.26 (3.71–4.70; 18). Palpal proportions: 55–70:211–250:195–242:179–350 μm . Frontal tubercle only slightly longer than wide, length 40–50 μm , up to twice as long as wide. Dorsal extension of eye long and parallel-sided, 6 facets wide near apex. Clypeus at the base 0.86 (0.68–1.00; 16) of the width of the antennal pedicel (apparent width, in part, due to slide preparation; in unflattened specimens always <1.0). Temporal setae 33 (26–46, in 2–3 rows, the the anterior series being about 2 times the length of posterior. Buccal sensilla, Fig. 1c.

Thorax. Anteprepronotum moderately projecting at the dorsal apex, laterally without setae. Mesoscutal tubercle moderately developed. Dorsocentral setae 36 (26–48; 17), mostly in two, but partially in three rows. Acrostichial setae 15 (12–17; 13), in two staggered rows. Prealar setae 7–13; supra-alar setae 1–2. Scutellum with 40 (32–77; 17) setae; posteriorly two rows of heavy setae and several strewed setae anteriorly.

Wing. Membrane with fine microtrichia visible at 100 X; R and R_{4+5} darkened, other wing veins pale. Wing length 3.77 (3.10–4.53; 23) mm; squama with 24 (20–41; 17) marginal setae. R with 35 (27–39; 17) setae; R_1 with 22 (20–43; 17) setae; R_{4+5} with 25 (15–91; 17) setae.

Legs. Sensilla chaetica: PII – 9 (6–10; 17); PIII – 11 (6–13; 11), on both tarsi in the apical one-third. Leg ratios: PI – 1.18 (1.07–1.27; 23); PII – 0.58 (0.55–0.62; 15); PIII – 0.70 (0.68–0.72; 15). Beard Ratio: PI – 6.32 (5.20–7.75; 20).

Abdomen. Genitalia, Figs. 1ab, 2a. Ninth tergal setae 6 (0–19; 45), usually in one paler patch, occasionally in two smaller patches, or lacking. Anal point short and moderately broad at the base, pale;



not strongly downcurved, Fig. 1b. Gc/GS ratio 1.08–1.48. Superior volsella usually only slightly curved, dark, appearing more strongly curved in flattened slide mounts, Fig. 3b. Inferior volsella moderately capitate in side view (Fig. 3c). Gonostyli usually strongly inflated and abruptly tapered at apex, Fig. 3a.



Fig. 2. *Chironomus utahensis*. a. male genitalia; b. Pupa, posterolateral spur of segment VIII.

Fig. 1. *Chironomus utahensis*. Male imago: a. male genitalia, dorsal view; b. anal point (note weak tongue-like ornamentation near dorsal apex); c. buccal structures (note labial sensilla and pilose tip of labial lonchus); Pupa: d. cephalic tubercles and frontal apotome; Larva: e. mentum and oral field; f. epipharyngeal apparatus and labral sensilla.

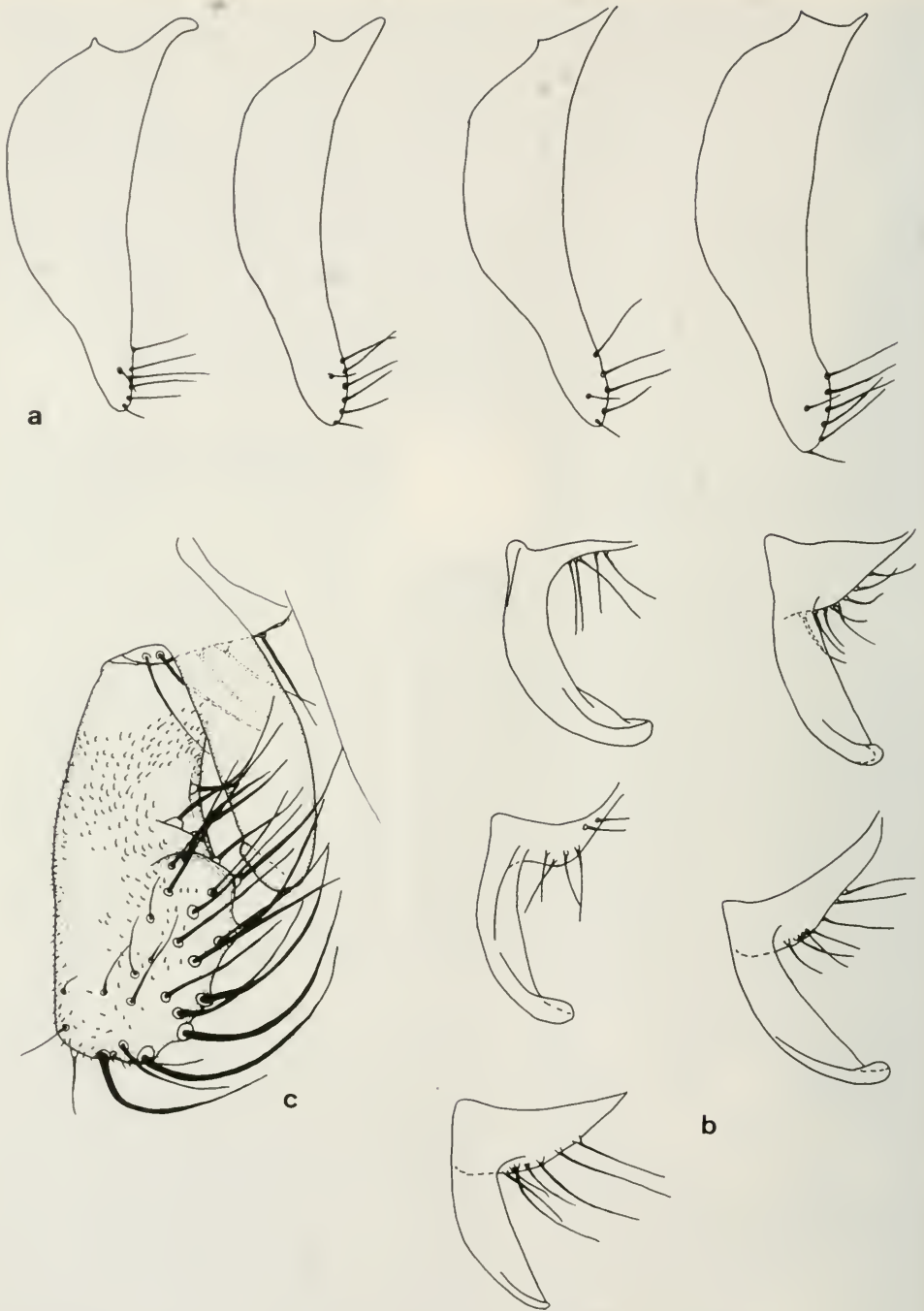


Fig. 3 *Chironomus utahensis*. a. variation of gonostylus; b. variation of superior volsella; c. posterolateral view of inferior and superior volsella.

Female

Coloration. Similar to male but ground color of thorax more yellowish with the vittae more distinct. Femora of all legs brownish with only the apices blackish; tibiae of P II, III brownish with the narrow bases and apices blackish; Ti of PI entirely blackish; tarsi entirely blackish.

Head. Antennal flagellomere proportions 179:133:133:125:211 μm . Palpal proportions 62:195:195:250 μm . Dorsal extension of eye short and moderately tapered to the rounded apex; six

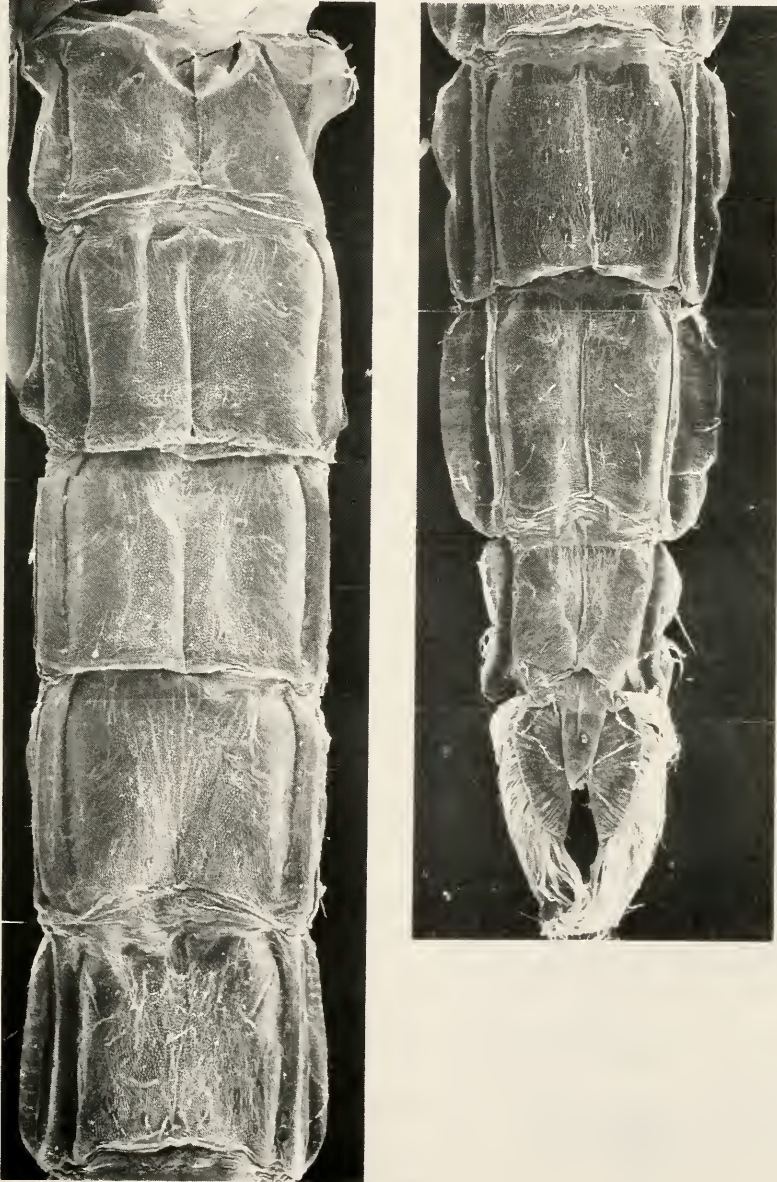


Fig. 4. *Chironomus utabensis*. Pupa. abdominal chaetotaxy.

facets wide at the third facet row from the apex. Ocular ratio 0.27. Clypeus at the base 1.73 times the width of the antennal pedicel; with 74–88 (3) setae. Temporal setae 31–36 (3).

Thorax. Anteprenotum moderately projecting on either side of the dorsal suture as in the male, laterally without setae. Mesoscutum tubercle distinct, as in the male. Dorsocentral setae 45–48 (3), in two to three rows at the greatest width. Acrostichial setae about 17, partially in two rows. Prealar setae 17–18 (3); supra-alar setae 1 (3). Scutellum with 75–77 (3) setae.

Wing. Membrane with microtrichia visible at 100 X. Costa, subcosta, and radial veins blackened, other veins pale. Wing length 3.89–4.53 (3) mm; squama with 33–41 (3) marginal setae. R with 38–39 (3) setae; R_1 with 36–43 (3) setae; R_{4+5} with 61–91 setae.

Legs. Sensilla chaetica of PII 111–123 (3); PIII 114–120 (3). Leg ratios: PI 1.07–1.21 (3); PII 0.51–0.54 (3); PIII 0.66–0.67 (3).

Genitalia. Very similar to *C. harpi* (cf. Fig. 5b).

Pupa

Male. Total length 8.22–9.67 (8) mm. Cephalothorax brownish-black, heavily papillose, cephalic tubercles, Fig. 1d. Respiratory organ with four main branches and numerous terminal branches. Abdomen pale, laterally with very weak dark, longitudinal stripes; posterolateral spur and swim fin margin dark.

Abdominal chaetotaxy, Fig. 4; hooks of second tergum pale; lateral hooks with long slender spinose tips; median hooks with shorter tips; many, but not all, hooks with a slight heel at the flexure; number of hooks, 90 (82–91; 8).

Posterolateral spur of eighth segment, Fig. 2b, with 6 (4–8) (16) spines. Eighth segment with five lateral, flattened setae, Fig. 2b; swim fin with 94 (88–100; 8) lateral swim setae.

Larva

Head. Capsule yellowish, with the tips of the mandibles, antennal pedicle, mentum, gular region, and occiput blackened. Ventral head length 186–198 μm .

Mentum, Fig. 1e, ventromental plate with 31–37 striae. Antenna, antennal length 182–198 μm .

Mandible. Basal tooth pale; with 2–3 medial denticles which are attenuate at the tips; pecten mandibularis with 10–14 setae; seta subdentalis short and lanceolate. Seta interna with four branches, similar to other members of the genus.

Dorsal head sclerites similar to other members of the genus; labral sclerites three and four with numerous microsclerites.

Oral field, Fig. 1ef. Ventral labral structures: Pecten epipharyngis with 11–13 almost uniform teeth, those in the center longer and evenly reduced in length laterally; SI pectinate; SII simple; chaeta media pectinate; other chaetae simple.

Maxilla. Blade of lacinia evenly tapered, smooth; lacinial chaeta simple; chaetulae of maxilla mostly rounded blades with a few of the smaller lateral chaetulae weakly fimbriate. Maxillary palp very similar to that of *C. harpi* n. sp. (cf. Fig. 7e).

Abdomen. Paired ventral tubuli of eleventh abdominal segment longer than posterior parapods; lateral tubuli of the tenth segment lacking. Posterior parapods with 14–15 brown claws. Anal cerci broader than high, each with six long setae.

Chironomus harpi, spec. nov. (author: J. E. Sublette)

Tendipes plumosus (L.), Harp and Campbell 1967: 260, ecology, distribution (misidentification).

Chironomus sp., Heaton 1951: 1, ecology.

Chironomus n. sp., Harp and Hubbard 1972: 48, ecology; Harp and Campbell 1973: 49, physiology.

Chironomus nr. *maturus* Bates and Stahl 1985: 127, ecology, physiology, life history; Zullo and Stahl 1988: 353, ecology, review of acid lakes midge fauna.



Fig. 5. *Chironomus barpi*. a. male genitalia, holotype; b. female genitalia, paratype.

Holotype male.

Type locality: Saline Co., 40 km SW Little Rock, Arkansas, Bauxite open-pit lake 4, T2S, R14W, SE¹/₄ S11, 21-III-70, George L. Harp, (in the collection of USNM). We are pleased to dedicate this new species to Dr. George L. Harp, Arkansas State University, who kindly sent us the original material.

Coloration. Ground color of head and thorax yellowish; antennal pedicels, anteprenotum, thoracic vittae, sternopleuron, postnotum, coxae, and abdomen blackish-brown; legs beyond coxae yellowish brown as is most of scutellum. A strong seasonal dimorphism is exhibited in the coloration with the holotype male and paratypes collected in March having an almost entirely black abdomen while the paratypes collected in May have a pronounced fasciate abdomen: tergum I with a median transverse fascia; tergum II with a basal brownish-black fascia and an apical yellowish fascia occupying about one-third of the tergum; terga III – IV with a dark basal and a pale apical fascia which is progressively broader posteriorly so that on tergum V there is only a narrow medial transverse dark fascia occupying less than one-third of the total length.

Legs of specimens in March (as evidenced by fully hardened females) entirely dark; in the May specimens the femora and tibiae are pale and Ta₁₋₃ of all legs mostly yellow with just the apices dark; Ta₄₋₅ of all legs dark.

Head. Antennal ratio 4.32 [3.88 (3.69–4.22; 5)]. Palpal proportions 55: 195:234:234 μ m. Frontal tubercle length 15 (31; 2) μ m. Dorsal extension of eye long and parallel-sided, 6 facets wide near apex; ocular ratio 0.17. Clypeus 0.75 of the width of the antennal pedicel; with 36 [32 (28–40; 7)] setae. Temporal setae 29 [35 (30–42, 7)].

Thorax. Anteprenotum narrowed towards the apex then slightly widened just before the apex. Mesoscutum tubercle small but distinct. Dorsocentral setae 28 [25 (21–30; 7)]. Acrostichial setae 17 [19 (16–20; 3)], in 1–2 staggered rows. Prealar setae 5 [5 (4–6; 7)]. Supra-alar setae 1 [1 (0–1; 7)]. Scutellum with 20 [29 (23–39)] setae.

Wing. Membrane with microtrichia visible at 100 X. Anterior wing veins darkened; r–m crossvein darkened; M₁₊₂, M₃₊₄, M, Cu, Cu₁, and An dusky, but paler than radial veins (paratype). Venarum ratio 1.01. Wing length 3.58 [3.20 (2.63–3.67; 4)] mm; squama with 29 [26 (23–41; 7)] marginal setae, in a partial doubled row. R with 26 [30 (17–34; 7)] setae; R₁ with 15 [17 (5–19; 7)] setae; R₄₊₅ with 10 [14 (4–22; 7)] setae].

Legs. Sensilla chaetica of PII – 9 [7 (5–8; 7)]; PIII – 7 [6 (4–8;)]. Leg ratios: PI – 1.40 [1.39 (1.33–1.43; 3)]; PII – 0.56 [0.59 (0.57–0.62; 6)]; PIII – 0.72 [0.71–0.73; 5]. Beard ratio: PI – 3.26 [3.36 (2.2–4.67; 3)].

Abdomen. Genitalia, Fig. 5a. Ninth tergal setae 5 [4 (2–9; 7)]. Superior volsella bluntly tipped, with a small recurved hook. Inferior volsella long and narrow.

Allotype female, Saline Co., Arkansas, Lake IV, collected with the holotype male (in the collection of USNM).

Coloration. As holotype male expect not teneral; thus, coloration is darker; legs are blackish.

Head. Antennal proportions 195:140:125:117:265 μ m. Palpal proportions 70:211:257:351 μ m. Length of frontal tubercle 31 μ m. Ocular ratio 0.16. Clypeal setae 39. Temporal setae 35, in a partial double row, reaching medial to the dorsal apex of the eye.

Thorax. Anteprenotum narrowed towards the dorsal apex but widened and projecting on either side of the median suture. Mesoscutum with weakly discernible median tubercle. Dorsocentral setae 48, in a staggered double to triple row which extend farther anterior than in the male. Acrostichial setae not visible in lateral slide mount. Prealar seta 5; supra-alar setae 2. Scutellum with a staggered posterior row of coarse setae and anteriorly with finer setae in an scattered pattern; total, 24 setae.

Wing. Membrane with microtrichia visible at 100 X. Wing veins darkened as the male, but more intensely so. Venarum ratio 1.05. Wing length 4.17 mm; squama with 43 marginal setae, in 2–3 rows; R with 40 setae; R₁ with 24 setae; R₄₊₅ with 60 setae.

Legs. Sensilla chaetica: PII – 67 in 1–2 rows, occupying most of Ta_1 ; PIII – 68 in 1–2 rows, occupying most of Ta_1 . Leg ratios: PI – 1.45; PII – 0.54; PIII – 0.70.

Abdomen. Genitalia, Fig. 5 b (paratype female).

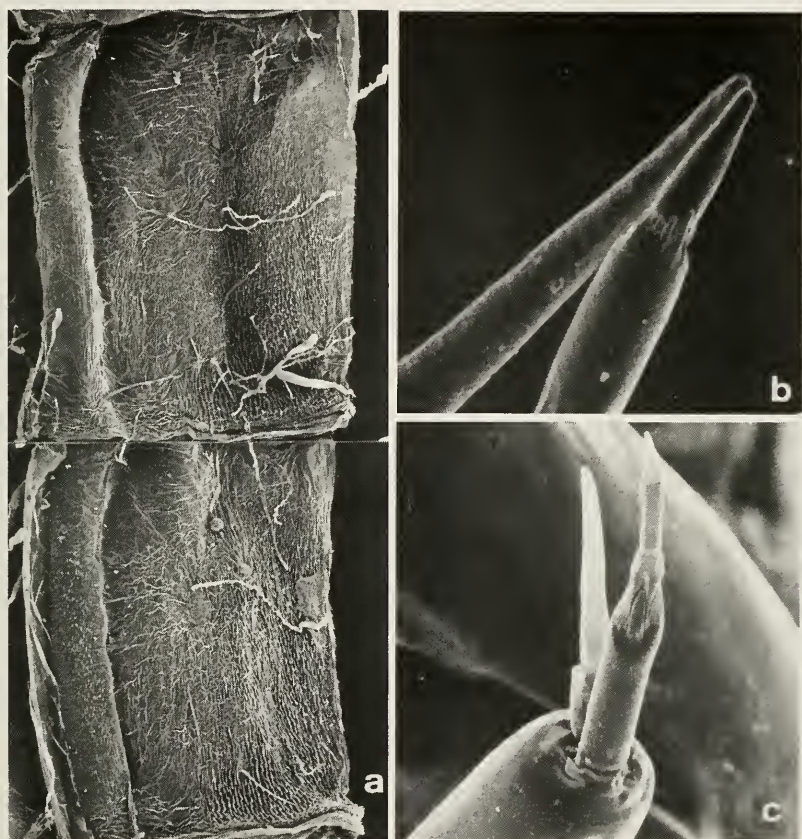


Fig. 6. *Chironomus harpi*. Pupa. a. chaetotaxy of tergum IV and V (dorsolateral). Larva. b. antennal apex, showing Lauterborn organ-like structures at the tip of segment 4; c. antenna, apical segments 2–5, showing Lauterborn organ-blade, and accessory blade.

Pupa

Coloration. Exuvial cephalothorax blackish-brown; abdominal terga I–V with dark chagrin over most of each tergum; VI with basal transverse band and two apical round patches of dark; swim chagrin; VII–VIII largely pale; fins dark; with a longitudinal dark stripe which becomes progressively broader posteriorly on both sides extending from II–VIII.

Total length 7.84–7.96 mm (3) (males) and 7.82–9.24 mm (4) (females). Recurved hooks of the second tergum 70 (64–88; 6). Posterolateral spur of segment VIII with 4 (1–8; 12) spines. Swim fin with 79 (62–98; 7) lateral flattened setae.

Abdominal chagrin and chaetotaxy, Fig. 6 a.

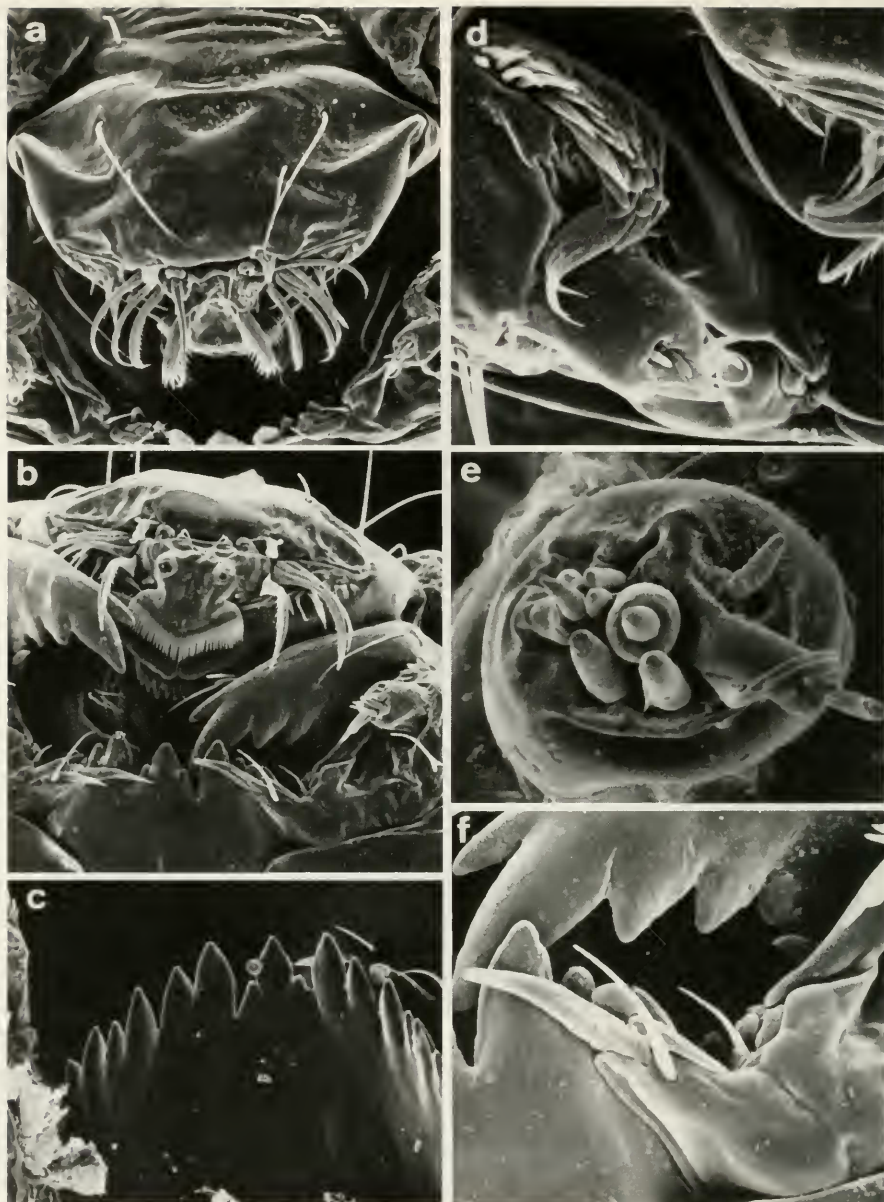


Fig. 7. *Chronomus harpi*. Larva. a. labrum, dorsofrontal view; b. oral field (SI and SII removed); c. mentum, ventral surface; d. detail of palpiger chaetulae; e. maxillary palpus, apical view; f. maxillary lacinia.

Larva

Head – Coloration mostly yellowish with tips of the mandibles, mentum, tips of premandibles, triangular sclerite und postoccipital margin blackish; posterior part of gula in front of postoccipital margin weakly infuscate.

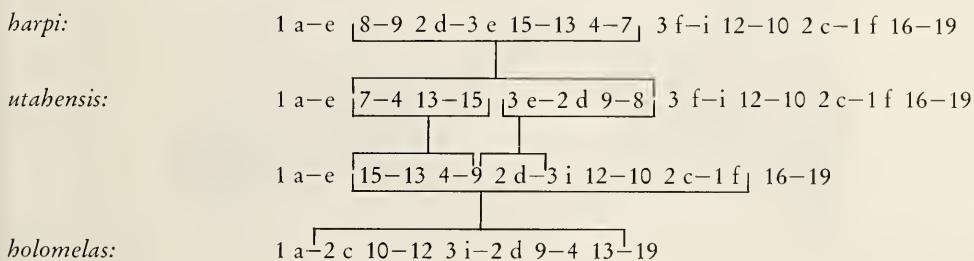
Ventral head length 306 (296–324; 5) μm . Labral structures, dorsofrontal view, Fig. 7a; anterior view, Fig. 7b; SI fimbriate on medial surface; SII elongate, filiform; SIII, SIV A, B of the usual position and shape as in other members of the genus; ChM progressively more weakly fimbriate laterally; teeth of Pe somewhat irregular in length.

Mentum. Fig. 7c, lateral teeth 4 and 5 subequal in length; tooth 6 much shorter. Ventromental plates, anterior margin smooth; with about 34 striae.

Mandible. With 2 subapical dorsal teeth, the more proximal of which is apically filiform; ventromedial basal tooth paler than other teeth; dorsomedial margin with 2–3 filiform teeth; seta subdentalis widest near middle, filiform at tip; pecten mandibularis with 14 sensilla trichoidea; with 4 fimbriate seate interna which are similar to those of other members of the genus.

Maxilla, Figs. 7d–f, chaetae of palpiger, Fig. 7d (note palmate structure near base of palpus). Palpus, Fig. 7e with a least 10 apparent sensillar structures; lacinia and associated blades, Fig. 7f; apical blade (chaeta) evenly attenuate from the maximum width near the base; dorsal blade shorter, of a similar shape but fimbriate on both margins; antaxial trichoid sensillum [“antaxial seta” (Aa) of Saether 1980] reaches to about the middle of the terminal lacinial blade.

Antenna, Figs 6b–c; note digitiform apparent sensilla at the apex of segment four, Fig. 6c, which resemble those of the Lauterborn organ.



Abdomen. Anterior parapods with a few claws weakly pectinate at tip; intermediate lobe scarcely developed. Lateral tubules present; ventral tubules subequal in length, extending beyond posterior parapods; about 15 claws of posterior parapods. Preanal papillae wider than high, with 2 posterior fine setae and 7 long terminal setae.

Karyotypes

Chromosome arm combination AB, CD, EF, G (*thummi*-complex). In both species nucleolus in arm D, not far from the centromere. In *C. utabensis* centromere of chromosome CD moderately heterochromatic, other centromeres also sometimes with slight heterochromatinization. In *C. harpi* centromeres not heterochromatinized. The chromosomes of *C. harpi* were figured by Yamamoto (1977) as an unnamed *Chironomus* species. His material has been examined in the present study.

Arms A (Figs 8ab): The pattern of *C. utabensis* can be derived from the ancestral pattern (*C. holomelas*) by three inversion steps. A further step leads to *C. harpi*.

Another inversion (1f–13) leads to *C. obtusidens* (Fig. 12), but this derivation differs from that offered by Keyl (1962), who had no knowledge of the other *decorus*-group species.

Arms B (Figs 8cd): The arm has remarkably dark bands in its terminal region, just distal to the large puff, sometimes referred to as a Balbiani ring, that is commonly found in arm B (e.g. Martin 1971, Wülker and Martin 1974). Dark bands can also be seen near the middle of the arm in *C. utabensis*, frequently flanked proximally by another puff. In *C. harpi*, distal part of the arm identical to that of *C. utabensis*. In the proximal part a group of only three bands is transferred to a position just adjacent to

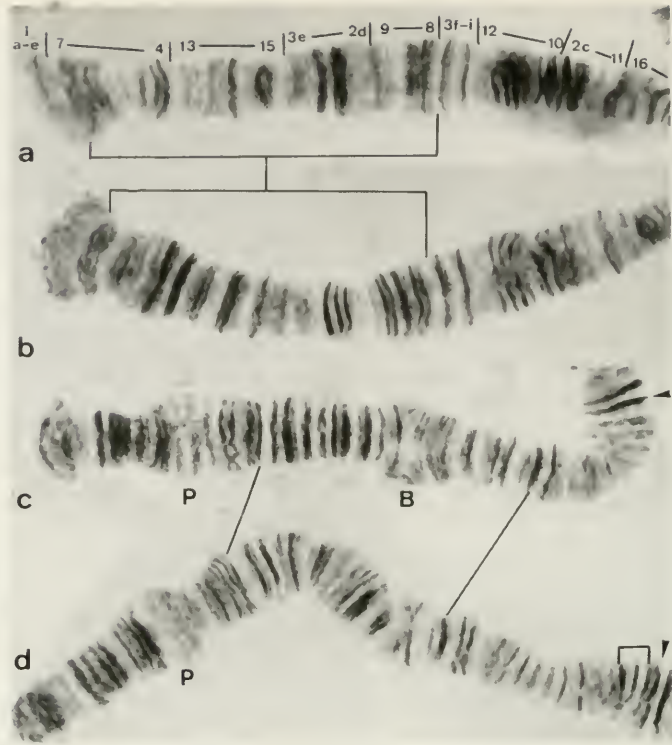


Fig. 8. *Chironomus utabensis*. Chromosome arm A (a) and B (c); *Chironomus harpi*, spec. nov. Chromosome arm A (b) and B (d). Brackets: limits of the inversion distinguishing the respective banding patterns. Some comparable bands connected by lines. B: Balbiani ring, P: puff, arrowhead: centromere.

the centromere (indicated by bracket in the figure). The other bands of this proximal region differ between *C. harpi* and *C. utabensis* in a complicated manner. The small more proximal Balbiani ring of arm B in *C. utabensis* seems to be missing in *C. harpi*.

Arms C (Figs 9ab): The "dumb-bell" group, which is characteristic of this arm (group a1-a4 of Keyl 1957), is in both species in a distal position, as in many other *Chironomus* species (see e. g. Wülker and Butler 1983). In *C. harpi* (Fig. 9b), a segment of about 17 bands, proximal to the middle of the arm in *C. utabensis*, occurs in inverted orientation in a more distal position in *C. harpi*, whereas the region of about 22 bands adjacent to this in the middle of the arm has the same orientation but is proximally located in *C. harpi*. This difference can be explained by a long inversion (X) concomitant with re-inversion of the included segment Y.

Arms D (Figs 9cd): Characterized in both species by the nucleolus near the centromere, and by two dark band groups distal to the nucleolus. In *C. harpi* (Fig. 9d), distal part identical with the standard sequence of *C. utabensis*. In the more proximal regions the relationships to *C. utabensis* seem to be complex since some band groups (Y, Z) can be recognized to occur in a different order, but while group Y retains the same orientation the two groups labelled X and Y are inverted relative to the *C. utabensis* sequence.

Arms E (Figs 10ab): Differs from the basic pattern found in *C. aberratus*, etc. (Wülker 1980), by a long inversion 12-7d, with the proximal break relatively close to the centromere. The characteristic "gap" in the banding pattern of arm E (group 11) is therefore transferred to about the middle of the arm. A short inversion in the middle of the arm leads to *C. harpi*.

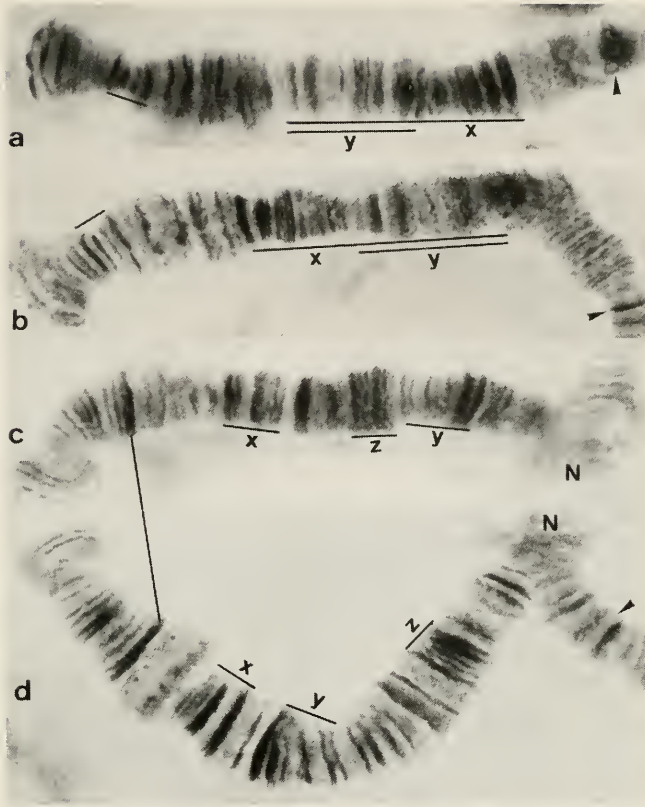
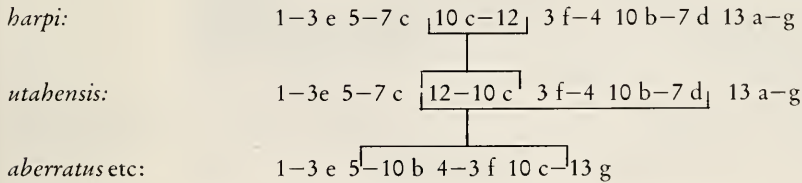


Fig. 9. *Chironomus utabensis*. Chromosome arm C (a) and D (c). *C. harpi*, spec. nov. Chromosome arm C (b) and D (d). Comparable band groups marked x and y (see text). N: nucleolus. Other symbols as Fig. 8.



The pattern for arm E of *C. utabensis* was proposed by Martin et al. (1979), although the position of band 7d was shown incorrectly.

Arms F (Figs 10cd): Most of the dark bands of the arm are in the distal region. The banding pattern of *C. utabensis* can be derived from the basic pattern of *C. piger* by three inversions. In determining the derivation of the banding pattern of *C. harpi* the orientation of group 10 is most important. This is a symmetrical group so that distinguishing between the alternatives of band sequence a-d or d-a is not presently possible. If it is assumed that the band sequence is a-d, the pattern of the arm can be derived from that of *C. utabensis* by 3 inversion steps. F2 of *C. utabensis* shares one inversion step with *C. harpi* (Fig. 12)

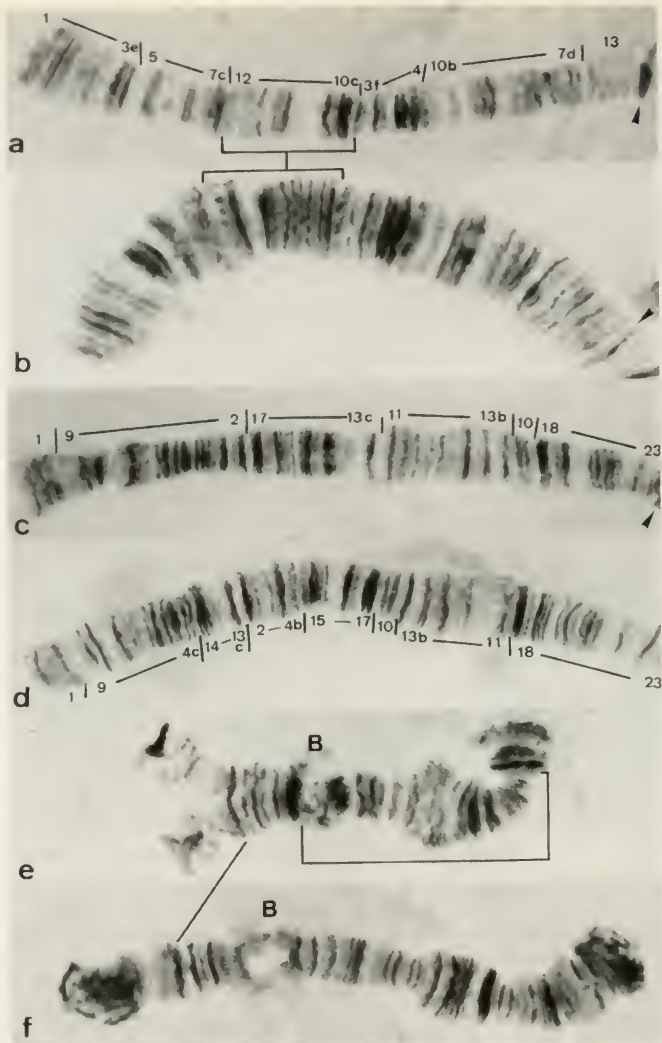
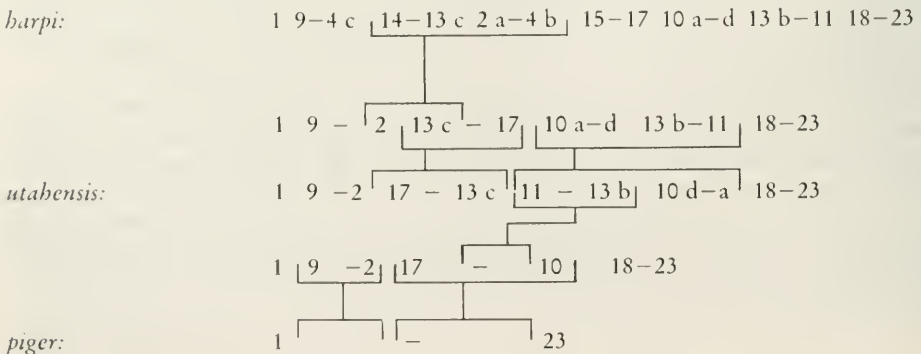


Fig. 10. *Chironomus utabensis*. Chromosome arm E (a), F (c) and G (e); *C. harpi*, spec. nov. Chromosome arm E (b), F (d) and G (f). Brackets in a b: approximate limits of the inversion distinguishing the two banding patterns. Bracket in e: limit of inversion resulting in sequence G2. Other symbols as Fig. 8.



Arms G (Figs 10ef): In both species long, with numerous bands. The two homologues are tightly paired with one end of the arm heterochromatinized. No nucleolus is present but there is a Balbiani ring about one third of the distance from the heterochromatinized end; many similarities of banding pattern of both species. However in *C. harpi* the bands near the Balbiani ring seem to be different or in a different arrangement.

Inversion Polymorphisms

Nine inversions have been represented in our material of *C. utabensis*, mostly from California, with only one occurring throughout the range of the investigated populations.

Arm A: A very short inversion of approximately the region 3 a–9, accompanied in many cells by the development of a large puff in the inverted sequence (not illustrated) was found heterozygous in a single individual from Klamath Lake, Oregon.

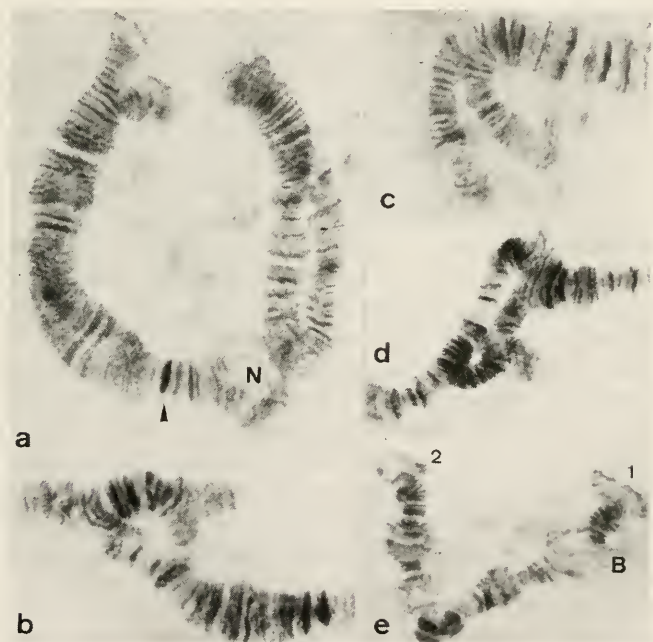


Fig. 11. *Chironomus utabensis*. Inversion heterozygotes. a. Arm C (left) heterozygous for the short terminal inversion and arm D (right) heterozygous for the long inversion distal to the nucleolus (N), from Lake Davis, Calif.; b. Arm C heterozygous for the distal inversion which includes the dumb bell figure, from near Wagner, S. D.; c. Arm D heterozygous for the short terminal inversion, from near Taylor, N. M.; d. Arm F heterozygous F1/F2, from Lake Davis, Calif.

Arm C: 1). A very short inversion at the distal end, partly including the “dumb bell” group (Fig. 11 a).

2). A longer inversion in the distal third of the arm which includes the “dumb bell” group (Fig. 11 b).

3). A very long, apparently complex inversion proximal of the “dumb bell” group (not illustrated), found in an individual from Benton Hot Springs, California.

Arm D: 1). A short inversion in the distal part of the arm (Fig. 11 c). The approximate limits of this inversion were given by Martin et al. (1979). 2). A long inversion of the region distal to the nucleolus (N) (Fig. 11 a).

Arm E: An inversion of the middle part of the arm (not illustrated) found in an individual from Silver Lake, California.

Arm F: Two overlapping inversions, 17–13 c and 14–9, in the distal part of the arm, give rise to the alternative sequence F2. The approximate banding pattern of this sequence is:

1 14–13 c 2–9 15–17 11–13 b 10 d–a 18–23. A heterozygote for F1/F2 is shown in Fig. 11 d.

Arm G: A large inversion covering over half of the arm which shifts the position of the Balbiani ring (B) (Fig. 11 e). One breakpoint appears to be adjacent to the Balbiani ring, the other about 10 bands from the right end of the arm.

Most of these inversions have been recorded predominantly from populations in California, Oregon and South Dakota. Only the short terminal inversion in arm D has been found as a polymorphism in New Mexico populations, where it appears to occur at low frequency in most populations, e. g. 7 % at Taylor Springs (Martin et al. 1979), 9 % at Upper Abbott Lake and 15 % at Eagle Nest Lake. This inversion also occurred frequently in the California and South Dakota populations, as did the two more distal inversion in arm C. The longer of these two was also found as a heterozygote in one individual from Ronan, Montana.

The long inversion in arm D was common in some populations in California, such as Lake Davis, in the egg mass from near Storrie and near Benton Hot Springs (with about a third of individuals heterozygous), as well as in the Klamath Lake population from Oregon. Larvae from these two latter populations were commonly heterozygous for the arm F inversion, with about a third of individuals heterozygous at Benton Hot Springs, and about half of the larvae heterozygous at Klamath Lake. As a result the alternative homozygote occurred in both populations. The frequency of the F2 sequence was 31 % at Benton Hot Springs and 49 % at Klamath Lake. In addition these two populations carried the alternative G2 sequence, this being the most common sequence, at a frequency of 83 %, at Klamath Lake and having a frequency of 23 % at Benton Hot Springs. Thus the Klamath Lake sample is relatively different from the majority of *C. utahensis* samples but is linked to them by the intermediate frequencies of the Benton Hot Springs sample. It is uncertain whether this represents some unusual feature of the ecology of these two populations, or whether there is a cline in the frequency of the arm F and G sequences from California to Oregon. Larvae from the egg mass collected near Storrie, California were heterozygous for G1 and G2, but this tells us nothing of the relative frequency of the two sequences in the population at this locality. In *C. harpi*, only one individual, in poor condition, from Saline County, Arkansas was heterozygous for arm G. The details of the inversion could not be determined because of the poor quality of the chromosomes. All other individuals were homozygous in all chromosomes.

Discussion

a) Morphology

The adult male of *C. utahensis* most closely resembles *C. atrella* (Townes) and *C. anthracinus* Zett. in general size and coloration. The genitalia are most similar to *C. anthracinus* but the anal point of that species is longer and darker and the superior volsella is straighter; the width of the clypeus of *C. anthracinus* is always greater than the width of the antennal pedicel, while in *C. utahensis* it is usually less.

The more northern species, *C. tuberculatus* (Townes) has a strong mesonotal tubercle, a dark, narrower anal point, and a more slender inferior volsella than *C. utahensis*.

The pupae of Nearctic *Chironomus* have not been adequately characterized to give a differential diagnosis at this time.

The larvae are similar to other members of the *decorus*-group. The combination of dark gular region, the dark antennal pedicel and pale basal mandibular tooth seems to be diagnostic.

The adult of *C. harpi* will key in Townes (1945) to [*Chironomus*] *decorus*; however, the almost straight, blunt tipped superior volsella is distinctly different than that species [cf. Townes, Fig. 136 A (compared with the holotype by J.E.S.)]. The coloration and general features resemble *C. maturus*; however, the genitalia of that species are distinctive in having a short, hooked, darkened superior volsella (cf. Sublette & Sublette 1974, Fig. 1)

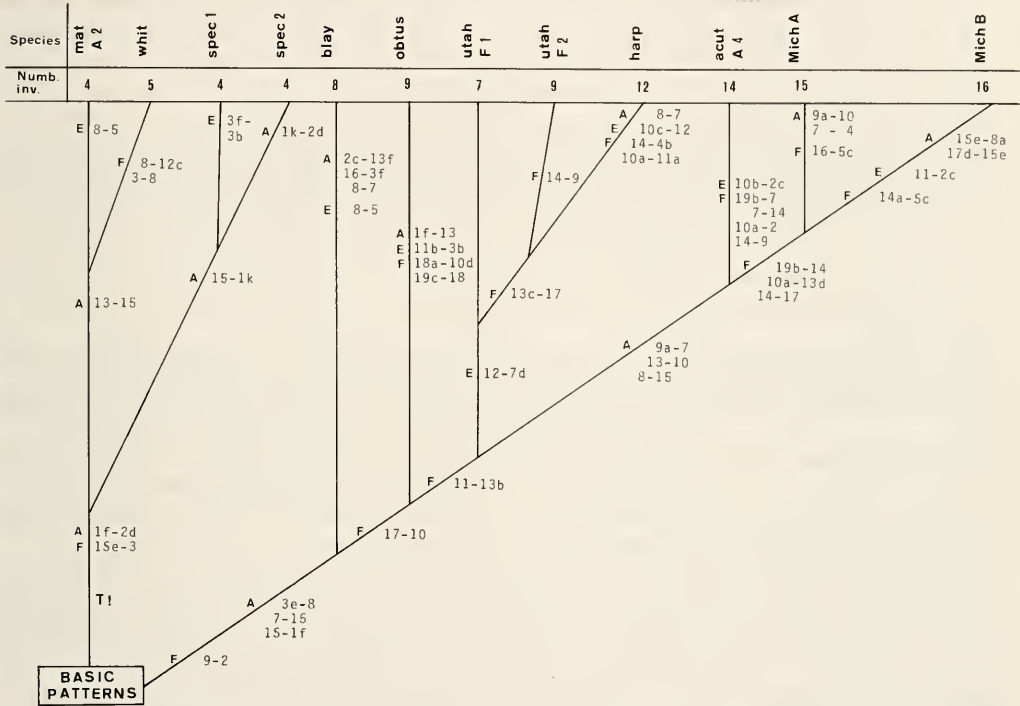


Fig. 12. Phylogenetic tree based on the banding patterns of chromosome arms A, E and F in the "*decorus*-group". The species of the *maturus*-complex, which are *decorus*-like as adults, are included at the left as an "outgroup". As "basic patterns", we are regarding here the Standard pattern of *C. holomelas* in arm A, inv. 10 b-3 f and 5-10 b from Standard in arm E and Standard *C. piger* in arm F (cf. Keyl 1962, Wülker 1980). Inversion polymorphism is not included (with exception of F2 in *C. utabensis* to show the similarities with *C. harpi*); instead, only the banding pattern with the shortest distance to the other species (e. g. A 4 in *C. acutiventris*) is shown. T! = whole arm translocation AB, EF-AF, BE; number of inversions = distance from "basic patterns" in arms A, E and F. acut - *C. acutiventris* (Wülker et al. 1983); blay - *C. "tentans"* Blaylock 1963, 1965 and own unpublished results. harp - *C. harpi*, spec. nov.; mat - *C. maturus* (Wülker and Martin 1974); Mich. A and Mich. B - unidentified species related to *C. decorus*, from Michigan (sequences previously unpubl.); obtus - *C. obtusidens* Goet. (Keyl 1962, modified as per text); spec. 1 and spec. 2 - European species of the *maturus*-complex (Wülker 1985); utah - *C. utabensis* Malloch; whit - *C. whitseii* (Wülker and Martin 1974).

b) Karyotypes

C. utabensis and *C. harpi* are cytologically closely related species. They share, as a synapomorphy, inversion 12g-7d in arm E and differ in arms A and E by one, in arm C by two, and in arm F by three inversion steps. The nucleolus, the puff in arm B and the Balbiani ring in arm G are in the same relative positions.

Both species belong to a karyosystematically unique, probably monophyletic, group of *Chironomus* species ("decorus-group"), which can be characterized, for instance, by the key inversion 9-2 in arm F (Figs 10cd and 12). To show the position of the two species in this group, a preliminary phylogenetic tree for chromosome arms A, E and F (roughly 40 % of the total band complement) is given in Fig. 12. Trees incorporating data for more than one arm are superior to "one-arm trees" (Wülker et al. 1986). Keyl (1962) was the first to produce a phylogenetic tree which combined the results for arms A and F of *Chironomus* species. The construction of the tree in Fig. 12 is based on the background of having completed a computer analysis (Wülker et al. 1984) incorporating recently 60 different banding patterns of arm A, 34 of arm E and 67 of arm F from all over the world (Wülker et al. in press). In the analysis, the frequencies or probabilities of neighborhoods of all single bands have been computed and the banding patterns arranged according to their probability. The pattern with the most common band neighborhoods is regarded as an "ancestor pattern". Such patterns are those of *C. bolomelas* in arm A, of *C. aberratus*, *C. piger* and *C. aprilinus* in arm E, and of *C. piger* in arm F. In addition, these patterns have a central position in Wagner networks of the respective arms (Keyl 1962), are found in the few species with a distribution over more than one continent, and are shared by more than one of the "complexes" of the genus (Wülker 1980). Furthermore the computer analysis shows how far the probability-values of a given pattern are from the respective ancestral pattern. It indicates which is the shortest and most probable connection between two or more patterns (thus following the parsimony principle) and, frequently, is able to correct details of preliminary phylogenetic models of the investigator.

The *maturus*-complex of *Chironomus*, which has the nearest karyological relationships to the *decorus*-group of the *thummi*-complex and has *decorus*-like adults, is used as an outgroup (sensu Hennig 1966).

The tree shows that *C. utahensis* represents the key inversions of the group (F 9-2, 17-10, 11-13b; A 15e-1f, 7d-15e, 3e-8a) and thus is basic for *C. acutiventris* in Europe and the two Michigan-species in North America, three taxa specialized by occurring in sandy bottoms of rivers and lakes and characterized by very high inversion polymorphism.

The information from *C. utahensis* necessitates corrections to previous attempts to derive arm A of *C. obtusidens* from that of *C. piger* (Keyl 1962) and arm A of *C. acutiventris* from that of *C. obtusidens* (Wülker et al. 1983). The very similar band groups 16a-c and 2c-1f were apparently confused in some *C. acutiventris* and Michigan-species patterns, and their position should be changed; as well, group 4-8 should read 4-7 8g-a. For example, the pattern of *C. acutiventris* 4 is then 1a-e 9a-e 2d-3e 15e-a 3f-i 12-10 4-7 8g-a 14-13 2c-1f 16-19 (compare Wülker et al. 1983).

One inversion (8-5 in arm E, also present in *C. stigmaterus*, Martin and Wülker 1974) occurs in both complexes. It may thus belong to the plesiomorphic "basic pattern", i. e. it must have existed before the separation of the *maturus*- and *thummi*-complexes (probably heterozygous with other basic patterns) and therefore occurs irregularly in one or the other homozygous configuration in recent species of both complexes.

Another inversion (8-7 in arm A) occurs twice at different places in the *decorus*-group, which seems contradictory to the principle of uniqueness of rearrangement events (improbability of identical two-break events such as inversions, Rothfels 1956). For such duplicities, one may propose two alternative explanations: 1) the inversions are plesiomorphic and may have been irregularly carried along during the evolution of patterns, 2) a non-random prevalence of particular breaks or inversions leads to independent incidence of these events in different places of the tree (see discussions in Martin 1979, Wülker 1980)

c) Inversion polymorphism

Since our results are based on a limited number of specimens from some of the localities, they may not be representative of the whole picture. Nevertheless, they confirm the finding by Martin et al.

(1979) of marked differences in the degree of inversion polymorphism between different populations of *C. utahensis*. The populations of California and Oregon were the most polymorphic, with inversions in arms A, C, D, E, F, and G. The South Dakota populations are somewhat less polymorphic, with inversions in arms C and D, while in New Mexico only the short terminal inversion in arm D has been found, generally in low frequency. Schaller and English (1976) make no mention of inversion polymorphism in their Arizona population, suggesting that it may be monomorphic. It is possible, then, that there is a cline of increasing polymorphism from east to west and from south to north. However further sampling would be needed to clarify the pattern of chromosomal polymorphism across the southwestern USA.

Acknowledgements

We are grateful to all our colleagues who contributed material to this investigation (see Materials examined). Mary F. Sublette, Pueblo, prepared the manuscript for publication; Mrs. R. Rössler, Freiburg, prepared the published chromosome photographs, while Mr. D. Paul, Melbourne prepared essential supplementary photographs.

References

- Bates, N. M & J. B. Stahl. 1985. Effect of pH and total ion concentration on growth rate of *Chironomus* nr. *maturus* larvae (Diptera: Chironomidae) from an acid strip-mine lake. Trans. Ill. Acad. Sci. 78: 127–132
- Blaylock, B. G. 1963. Chromosomal aberrations in a natural population of *Chironomus tentans* exposed to chronic lowlevel environmental radiation. — Ph. D. Thesis, Univ. of Tennessee
- 1965. Chromosomal aberrations in a natural population of *Chironomus tentans* exposed to chronic lowlevel radiation. — Evolution 19: 421–429
- Bonnell, D. E. & D. C. Mote. 1941. The Klamath midge. — J. econ. Ent. 34: 325
- 1942. Biology of the Klamath midge, *Chironomus utahensis* (Diptera Chironomidae). — Proc. Ent. Soc. Br. Columb. 39: 3–7
- Eggleton, F. E. 1931. A limnological study of the profundal bottom fauna of certain freshwater lakes. — Ecol. Monogr. 1: 231–332
- Harp, G. L. & R. R. Campbell. 1967. The distribution of *Tendipes plumosus* (Linné) in mineral acid water. — Limnol. Ocean. 12: 260–263
- 1973. Respiration rates of two midge species at different temperatures. — Ark. Acad. Sci. Proc. 27: 49–50
- & R. D. Hubbard. 1972. Limnology of four bauxite open-pit lakes. — Ark. Acad. Sci. Proc. 26: 47–51.
- Heaton, J. R. 1951. The ecology and succession of a group of acid and alkaline strip-mine lakes in Central Missouri. — M. S. Thesis, Univ. Missouri, Columbia, 143 p
- Hennig, W. 1966. Phylogenetic Systematics. — Univ. of Illinois Press, Chicago
- Keyl, H.-G. 1957. Untersuchungen am Karyotyp von *Chironomus thummi*. I. Karte der Speicheldrüsen-Chromosomen von *Ch. th. thummi* und die cytologische Differenzierung von der Subspecies *Ch. th. piger*. — Chromosoma 8: 739–756
- 1962. Chromosomenevolution bei *Chironomus*. II. Chromosomenumbauten und phylogenetische Beziehungen der Arten. — Chromosoma 13: 464–514
- & I. Keyl. 1959. Die cytologische Diagnostik der Chironomiden. 1. Bestimmungstabelle für die Gattung *Chironomus* auf Grund der Speicheldrüsenchromosomen. — Arch. Hydrobiol. 56: 43–57
- Malloch, J. R. 1915. The Chironomidae or midges of Illinois, with particular reference to species occurring in the Illinois River. — Bull. Ill. St. Lab. Nat. Hist. 10: 275–543
- Martin, J. 1971. A review of the genus *Chironomus* (Diptera, Chironomidae) IV. The karyosystematics of the *australis* group in Australia. — Chromosoma 35: 418–430
- 1979. Chromosomes as tools in taxonomy and phylogeny of Chironomidae (Diptera). — Ent. Scand. Suppl. 10: 67–74
- & W. Wülker 1974. A review of the genus *Chironomus* (Diptera, Chironomidae) VIII. *Chironomus stigmatismus* Say, Cytology. — Stud. Nat. Sci (Portales) 1 (11): 1–17

- J. E. Sublette & M. Sublette. 1979. Utilization of Chironomidae (Diptera) as a water quality indicator group in New Mexico. Part III. Karyosystematics of selected Chironomidae of New Mexico. — New Mexico Energy Inst. Rep. No. 32, p. 129–156
- W. Wülker & J. E. Sublette. 1974. Evolutionary cytology in the genus *Chironomus* Meigen. — Stud. Nat. Sci. (Portales, N. M.) 1 (12): 1–12
- Nabrotzky, F. V. 1968. Biology, behavior and control of some Utah gnats with special reference to *Tendipes utahensis* Malloch (Diptera — Tendipedidae). — M. S. Thesis, Univ. Utah, Salt Lake City, 63 pp.
- & D. M. Rees. 1968. Biology and behavior of the gnat *Tendipes utahensis* on the southeast shore of the Great Salt Lake, Utah. — Proc. 21th Ann. Meeting Utah Mosq. Abat. Assn. p. 45–46
- Rothfels, K. H. 1956. Black flies: sibilings, sex, and species grouping. — J. Heredity 47: 113–122
- Saether, O. A. 1980. Glossary of chironomid morphology terminology (Diptera: Chironomidae). — Ent. Scand. Suppl. No. 14, 51 pp.
- Schaller, L. 1972. An electrophoretic and cytogenetic study of *Chironomus utahensis* as found in Northern Arizona. — M. S. Thesis, N. Ariz. Univ., Flagstaff, 52 pp.
- & D. S. English. 1976. Electrophoretic and cytogenetic studies of *Chironomus utahensis*. — J. Heredity 67: 300–302
- Sublette, J. E. 1960. Chironomid midges of California. I. Chironominae, exclusive of Tanytarsini (=Calopsectrini). — J. Proc. U. S. Nat. Mus. 112: 197–226
- & M. F. Sublette. 1974. A review of the genus *Chironomus* (Diptera, Chironomidae) V. the *maturus*-complex. — Stud. Nat. Sci. (Portales, N. M.) 1 (8): 1–41
- 1979. Utilization of Chironomidae (Diptera) as a water quality indicator group in New Mexico. Part II. A synopsis of the Chironomidae of New Mexico. — N. M. Energy Res. Inst. Rept. 32, p. 53–128
- Townes, H. K. Jr. 1945. The Nearctic species of Tendipedini [Diptera, Tendipedidae (=Chironomidae)]. — Am. Midl. Nat. 34: 1–206
- Wülker, W. 1980. Basic patterns in the chromosome evolution of the genus *Chironomus* (Dipt.). — Z. zool. Syst. Evolutionsforsch. 18: 112–123
- 1985. Karyosystematics and morphology of two north European species of the *Chironomus maturus*-complex (Diptera: Chironomidae). — Entomol. Gener. 10: 125–132
- & M. G. Butler. 1983. Karyosystematics and morphology of northern *Chironomus* (Diptera: Chironomidae): Freshwater species with larvae of the *salinarius* type. — Ent. Scand. 14: 121–136
- & J. Martin. 1974. A review of the genus *Chironomus* (Diptera, Chironomidae) VI. Cytology of the *maturus*-complex. — Stud. Nat. Sci. (Portales, N. M.) 1 (9): 1–21
- G. Dévai & I. Dévai, in press. Computer assisted studies of Chromosome evolution in the genus *Chironomus* (Dipt.). Comparative and integrated analysis of chromosome arms A, E and F. — Acta Biol. Debrecina, Suppl. Oecol. Hungar.
- , G. Lőrincz & G. Dévai. 1984. A new computerized method for deducing phylogenetic trees from chromosome inversion data. — Z. zool. Syst. Evolutionsforsch. 22: 86–91
- , H. M. Ryser & A. Scholl. 1983. Revision der Gattung *Chironomus* Meigen (Diptera) VIII. Arten mit Larven des *fluviatilis*-Typs (*obtusidens*-Gruppe): *C. acutiventris* n. sp. und *C. obtusidens* Goetgh. — Rev. suisse Zool. 90: 725–745
- Yamamoto, K. D. 1977. A comparison of salivary gland chromosomes of *Chironomus* larvae of acid-polluted stripe-mine lakes. — M. S. Research Report, Southern Illinois University, Carbondale. 24 p.
- Zullo, S. J. & J. B. Stahl. 1988. Abundance, distribution, and life cycles of midges (Chironomidae: Diptera) in an acid stripe-mine lake in Southern Illinois. — Amer. Midl. Nat. 119: 353–365